Scion–rootstock interaction affects the physiology and fruit quality of sweet cherry

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Summary  Water relations, leaf gas exchange, chlorophyll a fluorescence, light canopy transmittance, leaf photosynthetic pigments and metabolites and fruit quality indices of cherry cultivars ‘Burlat’, ‘Summit’ and ‘Van’ growing on five rootstocks with differing size-controlling potentials that decrease in the order: Prunus avium L. > CAB 11E > Maxima 14 > Gisela 5 > Edabriz, were studied during 2002 and 2003. Rootstock genotype affected all physiological parameters. Cherry cultivars grafted on invigorating rootstocks had higher values of midday stem water potential (ΨMD), net CO2 assimilation rate (A), stomatal conductance (gs), intercellular CO2 concentration (Ci) and maximum photochemical efficiency of photosystem II (PSII) (Fv/Fm) than cultivars grafted on dwarfing rootstocks. The ΨMD was positively correlated with A, gs, and Ci. Moreover, A was positively correlated with gs, and the slopes of the linear regression increased from invigorating to dwarfing rootstocks, indicating a stronger regulation of photosynthesis by stomatal aperture in trees on dwarfing Edabriz and Gisela 5. The effect of rootstock genotype was also statistically significant for leaf photosynthetic pigments, whereas metabolite concentrations and fruit physicochemical characteristics were more dependent on cultivar genotype. Among cultivars, ‘Burlat’ leaves had the lowest concentrations of photosynthetic pigments, but were richest in total soluble sugars, starch and total phenols. Compared with the other cultivars, ‘Summit’ had heavier fruits, in contrast to ‘Van’ cherries. Nevertheless, ‘Van’ cherries had lower lightness, chroma and hue angle, representing redder and darker cherries, compared with ‘Summit’ fruits. In general, ΨMD was positively correlated with fruit mass and A was negatively correlated with lightness and chroma. These results demonstrate that: (1) water relations and photosynthesis of sweet cherry tree are mainly influenced by the rootstock genotype; (2) different physicochemical characteristics observed in cherries of the three cultivars suggest that regulation of fruit quality was mainly dependent on the cultivar genotype, although the different size-controlling rootstocks also had a significant effect.

Keywords: canopy light transmittance, chlorophyll a fluorescence, fruit physiochemical characteristics, gas exchange, leaf metabolites, photosynthetic pigments, Prunus avium, size-controlling rootstocks, water relations.

Introduction

Several reports have documented the relationships between various physiological parameters of grafted trees and fruit quality (Naor et al. 1995, Shackel et al. 1997, Naor 1998). These relationships are important from a horticultural point of view, because they provide a basis for selecting the best graft combination for particular environmental conditions and high fruit quality. Selection of an appropriate graft combination is crucial for the production of deciduous orchard species, because the scion–rootstock interaction influences water relations, leaf gas exchange, mineral uptake, plant size, blossoming, timing of fruit set, fruit quality and yield efficiency (Schmitt et al. 1989, Nielsen and Kappel 1996, Gonçalves et al. 2003).

In grafted trees, the control of plant size is mainly exerted through the rootstock. The mechanism by which the rootstock regulates scion vigor has not been identified (Sorce et al. 2002, Basile et al. 2003), although several potential dwarfing mechanisms have been studied, including the presence of small vessels that influence hydraulic conductivity (Simons and Chu 1984, Ussahatanonta and Simons 1988, Soumelidou et al. 1994, Salvatierra et al. 1998), lower total sap solute content (Jones 1984), low nutrient uptake capacity (Simons and Swiader 1985, Tagliavini et al. 1992, Nielsen and Kappel 1996, Rosati et al. 1997, Ebel et al. 2000) and reduced production of growth hormones (Chen et al. 1985, Sorce et al. 2002).

Rootstocks generally affect tree water relations. For cherry (Schmitt et al. 1989, Gonçalves et al. 2003), peach (Bongi et al. 1994, Basile et al. 2003) and apple (Giulivo and Bergamin...
trees grafted on invigorating rootstocks have consistently higher stem water potentials than trees grafted on dwarfing rootstocks. Moreover, in cherry (Shackel et al. 1997) and grapevine (Düring 1994; Iacono et al. 1998; Patakas et al. 2003), trees grafted on invigorating rootstocks have higher A and g_\text{e}. In grapevines, the graft combination also affects leaf photosynthetic pigments and metabolites (Bavaresco and Lovisolo 2000). Furthermore, fruit quality and maturity are reported to be affected by rootstock (Ezazhouani and Williams 1995). Autio and Southwick (1993) found differences in fruit color and fruit mass in apple grafted on different rootstocks, whereas Ferree (1992) and Meheriuk et al. (1994) found small or no difference in fruit soluble solids, skin color, firmness and mass in apple grafted on different rootstocks.

The northeast region of Portugal produces almost 40% of the Portuguese cherry crop. Although the cultivars most frequently grown in the region are considered to be well adapted to the local environment, there have been few field studies on the newer dwarfing rootstocks, which vary greatly in the physiological and morphological traits that determine their horticultural performance. We tested the following hypotheses: (1) size-controlling rootstocks affect the physiology of grafted sweet cherry trees; and (2) physicochemical characteristics of fruits are affected by the physiology of the scion–rootstock interaction. Specifically, the experiment was designed to evaluate stem water potential, leaf gas exchange, chlorophyll a fluorescence, light canopy transmittance, photosynthetic pigments, leaf metabolites and fruit quality of cherry cultivars ‘Burlat’, ‘Summit’ and ‘Van’ grafted onto rootstocks with contrasting size-controlling potentials, which decrease in the order Prunus avium L. > CAB 11E > Maxma 14 > Gisela 5 > Edabriz.

Materials and methods

Experimental trial

The study was carried out in Vila Real, in northeast Portugal (41°19′N and 7°44′W), at 470 m a.s.l., during 2002 and 2003. The climate is typical Mediterranean, with mild rainy winters and long, hot and dry summers. Mean annual rainfall is about 1100 mm, mainly from October to April. The warmest months are July and August and the coldest are December and January, with mean daily temperatures of 21–22 °C and 6–7 °C, respectively. Mean annual sunshine values over a 30-year period are 2392 h, the lowest monthly values (100 h) occurring in December and the highest (342 h) in July.

The soil is a deep (> 100 cm) sandy loam, dystric ardic anthroposol, pH 4.7, with an organic matter content of 1.5%, a high content of fine sand (0.2–0.02 mm), a high content of K_2O (150–200 mg kg^{-1}) and a medium content of P_2O_5 (50 – 100 mg kg^{-1}).

Three cultivars of sweet cherry trees (Prunus avium) were each grafted on five different rootstocks. The cultivars were: early-maturing ‘Burlat’, and the mid- to late-maturing ‘Summit’ and ‘Van’, and the rootstocks were: Prunus avium (vigorous), CAB 11E (clone of Prunus cerasus L.; semi-vigorous) Maxma 14 (Prunus avium × Prunus mahaleb L. hybrid; semi-dwarfing), Gisela 5 (Prunus cerasus × Prunus canescens Bois. hybrid; dwarfing) and Edabriz (clone of Prunus cerasus; very dwarfing). In 1999, trees were planted in a north–south orientation with rows 5.5 m apart. Within rows, trees were spaced according to the vigor of the rootstock: 5.5, 5.0, 4.5, 4 and 3.0 m for Prunus avium, CAB 11E, Maxma 14, Gisela 5 and Edabriz, respectively. Routine disease and pest control treatments were provided according to a commercial protocol for fruit production. The cherry orchard was drip-irrigated daily during May and September and periodically fertilized. The trees were not pruned in the summer during the experiment.

Water relations

Predawn (Ψ_{pd}) and midday stem water potentials (Ψ_{md}) of grafted cherry trees were determined on four dates (June 21 and July 8, 2002 and June 11 and July 9, 2003). Stem water potential (Ψ_{stem}) was measured on fully expanded healthy leaves. Branches were placed in black polyethylene bags that were wrapped in aluminum foil for at least 90 min before measurements, to allow leaf water potential to equilibrate with Ψ_{stem}. We measured Ψ_{stem} with two pressure chambers (ELE International, Bedfordshire, England) as described by Scholander et al. (1965). In all cases, leaves were placed in the chamber within a few seconds after excision. Eight measurements of Ψ_{stem} by the scion–rootstock combination were made during each diurnal period.

Gas exchange and chlorophyll a fluorescence

On July 9, 2003, leaf gas exchange rates were measured with a portable gas exchange system (ADC-LCA-3, Analytical Development, Hoddesdon, U.K.) and a leaf chamber clip (ADC-PLC, surface = 6.25 cm², volume = 16 cm³) with a quantum sensor, air temperature and humidity sensors. The gas exchange unit was operated in the open mode at a flow rate of 300 ml min^{-1} and an ambient CO_2 partial pressure of 35–37 Pa. Twelve measurements were made on fully expanded healthy leaves in the morning (0900–1100 h) and afternoon (1400–1600 h). Net CO_2 assimilation rate (A), stomatal conductance (g_\text{s}) and intercellular CO_2 concentration (C_i) were estimated from the gas exchange measurements with the equations of von Caemmerer and Farquhar (1981). Intrinsic water-use efficiency was calculated as the ratio of A to g_\text{s} (A/g_\text{s}) (Düring 1994). While measurements were being made, photosynthetic photon flux ranged between 1830 and 1960 µmol m^{-2} s^{-1}, air temperature ranged between 30.4 and 34.1 °C and air vapor pressure deficits were around 2.4 and 3.1 kPa, in the morning and afternoon, respectively.

Maximum photochemical efficiency of PSII in dark-adapted leaves (F_{v}/F_{m}), minimal (F_{o}) and maximal fluorescence (F_{m}) at open and closed PSII reaction centers, respectively, and variable fluorescence (F_{v}), were determined around midday on attached intact leaves similar to those used for gas exchange measurements with a portable chlorophyll fluorometer (Plant Stress Meter, BioMonitor SCI AB, Umeå, Sweden), as described by Öquist and Wass (1988). Before measurements,
Canopy light transmittance (%PFDt) values were taken as an indirect indicator of canopy size (cf. Dufrêne and Bréda 1995). Midday %PFDt was calculated as the ratio of photosynthetic photon flux (PPF) measured horizontally below and above the canopy with a Sunfleck Ceptometer (Model SF-80, Decagon Devices, Cambridge, U.K.), as described by Campbell (1986). Eight means of %PFDt were determined per scion–rootstock combination. Each mean consisted of 10 measurements taken over the ground area shaded by the canopy.

Photosynthetic pigments and metabolite assays
Leaf discs (1.57 cm²) taken from fully expanded leaves of comparable physiological age were frozen in liquid N₂ and stored at –80 °C until analyzed. Chlorophyll a (Chloₐ) and b (Chloₐb) were extracted in 80% acetone and quantified spectrophotometrically (Sesták et al. 1971). Total carotenoids were extracted with the chlorophylls and determined with the equations of Lichtenthaler (1987).

Total soluble sugars were extracted by heating leaf discs in 80% ethanol (Irigoyen et al. 1992) and incubating 200 µl of the extract with 3 ml of fresh anthrone in a boiling water bath for 10 min. After cooling, the absorbance at 625 nm was determined. Starch was extracted from the ethanol-insoluble fraction with 30% perchloric acid, as described by Osaki et al. (1991), and the concentration determined by the anthrone method, as described above. Glucose was used as the standard for both total soluble sugars and starch.

The concentration of total phenolics in leaf extracts was determined on the same extract used for pigment analysis by the Folin-Ciocalteu procedure (Singleton and Rossi 1965), with the modifications described by Heinonen et al. (1998).

Leaf discs for the photosynthetic pigment and metabolite assays were used to calculate leaf mass per unit area (LMA) as: LMA = DM/LA (g cm⁻²), where DM is dry mass, measured after drying at 70 °C to constant mass, and LA is the leaf disc area. Eight leaves per scion–rootstock interaction were collected (July 8, 2002 and July 9, 2003) to determine photosynthetic pigment and metabolite concentrations. Values of these parameters were expressed on a DM basis.

Fifteen treatments were laid out as a two-factor experiment with five rootstocks and three cultivars arranged in a randomized complete block design with two replications. Each replication comprised six trees per treatment. The measurements were made on two representative trees of each scion–rootstock combination. Data were subjected to analysis of variance (ANOVA) and means were separated by Duncan’s significant difference test, when ANOVA indicated significant (P < 0.05) variable effects. The contribution of each factor to the global variation was calculated according to a fixed effects model (Snedecor and Cochran 1967).

A Fisher correlation analysis including all parameters was also performed. A Principal Component Analysis (orthotran/varimax) applied to 20 variables allowed us to identify a subset of characters that separated the genotypes to the maximum and to identify the relative contribution of each variable to their separation.

Statistics

Water relations
There were no significant differences (P > 0.05) in Ψ₂₀ values between rootstocks, cultivars or cultivar–rootstock combinations (Table 1), whereas there was high variation in Ψ₅₀ values between rootstocks (P < 0.01), cultivars (P < 0.01) and cultivar–rootstock combinations (P < 0.05). For example, on July 9, 2003, Ψ₅₀ ranged from –1.17 MPa in ‘Summit’ grafted on CAB 11E to –1.71 MPa in ‘Van’ on Gisela 5 (Table 2). On average, Ψ₅₀ reached lower values (down to –1.71 MPa) in trees on the dwarfing rootstocks Edabriz and Gisela 5 than in trees on the invigorating rootstocks Prunus avium, CAB 11E and Maxma 14. Among the cultivars, ‘Summit’ had the highest Ψ₅₀, except when grafted on Edabriz, where it was similar (–1.59 MPa) to that of the other cultivars. As expected, Ψ₅₀ decreased from predawn to midday, and the low Ψ₅₀ values coincided with the time of maximum atmospheric evaporative demand. The greatest decreases in Ψ₅₀ from predawn to midday were recorded in ‘Burlat’ and ‘Summit’ grafted on Edabriz and in ‘Van’ on Gisela 5.
Gas exchange and chlorophyll a fluorescence

Diurnal patterns of the physiological parameters measured were similar throughout the season and in the two studied years, so only the data obtained on July 9, 2003 are presented. There were significant differences ($P < 0.001$) in the leaf gas exchange parameters ($A$, $g$, $C_i$ and $A/g_s$) between rootstocks, but not between cultivars or cultivar × rootstock combinations, except for $A$ ($P < 0.05$) in the morning (Table 1). In both the morning and afternoon, higher values of $A$, $g$, and $C_i$ were observed in trees on the invigorating rootstocks Prunus avium, CAB 11E and Maxma 14 than in trees on the dwarifying rootstocks (Figure 1). Trees grafted on Edabriz were the exception, with morning $A$ of trees grafted onto dwarifying rootstocks being similar to the values measured in trees grafted on invigorating rootstocks. For every scion–rootstock combination studied, $A$, $g$, and $C_i$ were consistently higher in the morning than in the afternoon. The greatest diurnal decreases in $A$ were in trees on dwarifying rootstocks Edabriz and Gisela 5: the maximum diurnal reduction in $A$ was 53% in ‘Van’ grafted on Gisela 5, which had a minimum value of 6 µmol m$^{-2}$ s$^{-1}$. On the other hand, trees grafted on dwarifying rootstocks had the highest $A/g_s$ of the graft types (Figure 1). Values of $A/g_s$ increased from the morning to the afternoon, mainly in trees on Edabriz, ranging from 32 to 42 µmol mol$^{-1}$.

There were significant differences ($P < 0.05$) in the $F_v/F_m$ between rootstocks, but not between cultivars or cultivar × rootstock combinations.
rootstock combinations (Table 1). Moreover, $F_0$, $F_m$ and $F_v$ varied significantly ($P < 0.001$) among rootstocks, and $F_m$ and $F_v$ differed ($P < 0.01$) among cultivar × rootstock combinations (Table 1). Generally, $F_v / F_m$, $F_0$, $F_m$ and $F_v$ were lower in trees on dwarfing Edabriz and Gisela 5 than in trees on invigorating Prunus avium, CAB 11E and Maxma 14 (Table 3).

Canopy light transmittance

Midday %PFD, varied significantly ($P < 0.001$) between rootstocks, cultivars and cultivar–rootstock combinations (Table 1). Values of %PFD, were always higher in cultivars grafted on dwarfing rootstocks Edabriz and Gisela 5 than in trees on invigorating rootstocks (Table 3). Among the rootstocks, trees grafted on invigorating rootstocks had the highest starch and total phenolic concentrations (Table 6).

Table 2. Effects of cherry cultivars and rootstocks on stem water potential at predawn ($\Psi_{PD}$) and midday ($\Psi_{MD}$) measured on July 9, 2003. Means (n = 8) followed by the same letter are not significantly different at $P < 0.05$ (Duncan’s test).

<table>
<thead>
<tr>
<th>Graft combinations</th>
<th>$\Psi_{PD}$ (MPa)</th>
<th>$\Psi_{MD}$ (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cultivar</td>
<td>Rootstock</td>
<td></td>
</tr>
<tr>
<td>'Burlat'</td>
<td>Edabriz</td>
<td>–0.16</td>
</tr>
<tr>
<td></td>
<td>Gisela 5</td>
<td>–0.28</td>
</tr>
<tr>
<td></td>
<td>Maxima 14</td>
<td>–0.39</td>
</tr>
<tr>
<td></td>
<td>CAB 11E</td>
<td>–0.23</td>
</tr>
<tr>
<td></td>
<td>Prunus avium</td>
<td>–0.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>–1.53</td>
</tr>
<tr>
<td>'Summit'</td>
<td>Edabriz</td>
<td>–0.34</td>
</tr>
<tr>
<td></td>
<td>Gisela 5</td>
<td>–0.20</td>
</tr>
<tr>
<td></td>
<td>Maxima 14</td>
<td>–0.27</td>
</tr>
<tr>
<td></td>
<td>CAB 11E</td>
<td>–0.22</td>
</tr>
<tr>
<td></td>
<td>Prunus avium</td>
<td>–0.25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>–1.59</td>
</tr>
<tr>
<td>'Van'</td>
<td>Edabriz</td>
<td>–0.24</td>
</tr>
<tr>
<td></td>
<td>Gisela 5</td>
<td>–0.22</td>
</tr>
<tr>
<td></td>
<td>Maxima 14</td>
<td>–0.22</td>
</tr>
<tr>
<td></td>
<td>CAB 11E</td>
<td>–0.22</td>
</tr>
<tr>
<td></td>
<td>Prunus avium</td>
<td>–0.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>–1.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Photosynthetic pigments and metabolites in leaves

Among the rootstocks, significant differences ($P < 0.01$) in total chlorophyll and total carotenoid concentrations and in ($P < 0.05$) LMA and chlorophyll a to chlorophyll b ratio (Chl a / Chl b) were observed (Table 1). Higher values of total chlorophyll, total carotenoids and Chl a / Chl b were always observed in the leaves of cultivars grafted on dwarfing rootstocks Edabriz and Gisela 5 (Table 5) than on invigorating rootstocks. Starch and total phenolic concentrations varied among cultivars ($P < 0.05$), rootstocks ($P < 0.001$) and cultivar–rootstock combinations ($P < 0.01$), whereas total soluble sugar concentrations did not vary significantly ($P > 0.05$) with cultivar, rootstock or scion–rootstock combination (Table 1).

There were significant differences in LMA, photosynthetic pigment concentrations ($P < 0.001$) and in the Chl a / Chl b ratio ($P < 0.05$) between cultivars (Table 1). 'Van' leaves had the highest concentrations of total chlorophyll and total carotenoids, approximately 30% higher than 'Burlat' leaves, although 'Van' had the lowest LMA (Table 5). On average, 'Summit' had the highest Chl a / Chl b (3.850) and 'Burlat' the lowest (3.091). Cultivar, rootstock and cultivar–rootstock combinations had no influence on total chlorophyll/total carotenoids (Table 1).

There were significant differences in starch concentrations between cultivars ($P < 0.001$) and rootstocks ($P < 0.05$) (Table 1). Total phenolic concentrations varied among cultivars ($P < 0.05$), rootstocks ($P < 0.001$) and cultivar–rootstock combinations ($P < 0.01$), whereas total soluble sugar concentrations did not vary significantly ($P > 0.05$) with cultivar, rootstock or scion–rootstock combination (Table 1). Among the rootstocks, trees grafted on invigorating rootstocks had the highest starch and total phenolic concentrations (Table 6).
Among the cultivars, starch was the main metabolite in leaves of ‘Burlat’ and ‘Summit,’ whereas ‘Van’ leaves had similar concentrations of starch, total phenolics and total soluble sugars. ‘Burlat’ leaves were richest in total soluble sugars, starch and total phenolics, whereas ‘Van’ leaves had the lowest concentrations of total soluble sugars, starch and total phenolics, with 47% less starch than ‘Burlat’ (Table 6).

**Fruit quality**

The basic characteristics of the cherries varied significantly (P < 0.001) with cultivar, rootstock and cultivar–rootstock combinations (Table 1). In general, the effect of cultivars accounted for the highest percentage of total variation in the fruit quality parameters (Table 1). Fruit mass was highest (> 10.3 g) in ripe cherries from ‘Summit,’ whereas fruits of the other cultivars had similar masses (always < 7.8 g) (Table 7). At harvest, the epidermis of ‘Burlat’ cherries had low firmness, whereas high firmness values were measured in ‘Van’ fruits (Table 7). However, firmness varied with cultivar–rootstock combination, particularly in ‘Burlat,’ which had soft fruits when grafted on CAB 11E (1.2 kgf cm⁻²) and relatively firm fruits when grafted on Gisela 5 and Prunus avium (around 1.8 kgf cm⁻²) (Table 7). The concentration of soluble sugars was highest in cherries from ‘Van’ trees on Edabriz (21.9 °Brix), but was particularly low (< 13.5 °Brix) in ‘Burlat’ grafted on dwarfing Gisela 5 and Edabriz and on invigorating Prunus avium (Table 7). ‘Burlat’ cherries contained lower titratable acidity (< 73 meq l⁻¹) than ‘Van’ cherries (> 97 meq l⁻¹) and ‘Summit’ fruits, which had intermediate acidity (Table 7). Rootstock had little effect on the titratable acidity and pH of the fruits. Among cultivar–rootstock combinations, fruits of ‘Burlat’ and ‘Summit’ grafted on invigorating rootstocks had the highest soluble sugar concentrations. Among ‘Van’ fruits, the highest soluble sugar concentrations were found in ‘Van’ grafted on dwarfing rootstocks (Table 7).

Fruit chromatic characteristics are shown in Table 8. There were significant differences in luminosity, chroma and hue...
angle ($P < 0.001$) among cultivars, rootstocks and cultivar–rootstock combinations (Table 1). At harvest, ‘Van’ cherries always had lower luminosity, chroma and hue angle, representing redder and darker cherries than ‘Summit’ and ‘Burlat’ cherries (Table 8). Cherries from ‘Burlat’ and ‘Summit’ grafted on dwarfing Edabriz and Gisela 5 generally had higher luminosity than cherries from trees on invigorating rootstocks.

### Relationship between principal physiological, biochemical and quality parameters

A principal component analysis (orthotran/varimax) between physiological parameters ($\Psi_{MD}$, $A$, $g_s$, $C_i$, $F_v/F_m$ and $%PFD_t$), photosynthetic pigments (total chlorophyll and total carotenoids), leaf metabolites (starch and total phenolics), LMA and fruit quality parameters (mass, firmness, titratable acidity, pH, soluble sugars, luminosity, chroma and hue angle) (Figure 2) measured in each cultivar–rootstock combination during the 2003 season was used to extract two main factors. The chromatic characteristics (luminosity, chroma and hue angle), pH and LMA, seemed to correlate well with factor 1, which accounted for about 27% of the overall variance, and were more dependent on cultivar genotype. The fruit variables mass, soluble sugars and titratable acidity were also more dependent on factor 1. Several physiological variables ($A$, $g_s$, $C_i$ and $\Psi_{MD}$) of sweet cherry trees were strongly correlated with factor 2, which accounted for about 23% of the overall variance. These four physiological variables seemed to be associated with the vigor of the tree and were mainly influenced by rootstock genotype, being consistently higher in trees grafted on invigorating rootstocks than in trees grafted on dwarfing rootstocks (Figure 1, Table 2). Intrinsic water-use efficiency was positioned on the opposite side to the $A$, $g_s$, $C_i$ and $\Psi_{MD}$ grouping. Trees on dwarfing Edabriz and Gisela 5 had the highest $A/g_s$ values (Figure 1). Foliar concentrations of starch and total phenolics and $%PFD_t$ correlated well with factor 2, and were highly dependent on rootstock genotype. The variables total chlorophyll, total carotenoids and firmness varied with both main factors. The $F_v/F_m$ ratio varied almost independently of cultivar and rootstock genotype (Figure 2).

### Discussion

**Effect of size-controlling rootstocks in the physiology of grafted trees**

Rootstock genotype significantly affected $\Psi_{MD}$ of cherry cultivars but not $\Psi_{PD}$ (Table 1), perhaps indicating complete over-

### Table 7. Effects of cultivar and rootstock on quality indices of cherries measured at harvest 2003.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Rootstock</th>
<th>W (g)</th>
<th>$F$ (kgf cm$^{-2}$)</th>
<th>SS ($^{\circ}$Brix)</th>
<th>pH</th>
<th>TA (meq l$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘Burlat’</td>
<td>Edabriz</td>
<td>6.33 a</td>
<td>1.48 b</td>
<td>13.38 a</td>
<td>4.16 fg</td>
<td>62.53 a</td>
</tr>
<tr>
<td></td>
<td>Gisela 5</td>
<td>7.79 b</td>
<td>1.77 de</td>
<td>13.03 a</td>
<td>4.36 i</td>
<td>70.07 b</td>
</tr>
<tr>
<td></td>
<td>Maxima 14</td>
<td>7.56 b</td>
<td>1.64 bcd</td>
<td>15.47 b</td>
<td>4.14 ef</td>
<td>72.57 b</td>
</tr>
<tr>
<td></td>
<td>CAB 11E</td>
<td>7.31 b</td>
<td>1.18 a</td>
<td>15.36 b</td>
<td>4.30 h</td>
<td>70.37 b</td>
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<tr>
<td></td>
<td><em>Prunus avium</em></td>
<td>7.60 b</td>
<td>1.74 de</td>
<td>13.47 a</td>
<td>4.20 g</td>
<td>67.43 a</td>
</tr>
<tr>
<td>‘Summit’</td>
<td>Edabriz</td>
<td>10.70 cd</td>
<td>2.40 f</td>
<td>13.87 a</td>
<td>4.11 de</td>
<td>82.73 c</td>
</tr>
<tr>
<td></td>
<td>Gisela 5</td>
<td>10.32 c</td>
<td>1.81 de</td>
<td>15.59 b</td>
<td>4.14 ef</td>
<td>85.93 c</td>
</tr>
<tr>
<td></td>
<td>Maxima 14</td>
<td>11.12 de</td>
<td>1.54 bc</td>
<td>18.05 d</td>
<td>4.01 b</td>
<td>92.10 d</td>
</tr>
<tr>
<td></td>
<td>CAB 11E</td>
<td>11.57 ef</td>
<td>1.67 bcd</td>
<td>16.70 c</td>
<td>4.04 b</td>
<td>104.67 f</td>
</tr>
<tr>
<td></td>
<td><em>Prunus avium</em></td>
<td>11.87 f</td>
<td>1.91 e</td>
<td>15.71 b</td>
<td>4.05 bc</td>
<td>93.00 d</td>
</tr>
<tr>
<td>‘Van’</td>
<td>Edabriz</td>
<td>7.59 b</td>
<td>2.46 f</td>
<td>21.90 f</td>
<td>4.08 cd</td>
<td>102.37 ef</td>
</tr>
<tr>
<td></td>
<td>Gisela 5</td>
<td>7.60 b</td>
<td>2.38 f</td>
<td>20.08 e</td>
<td>4.03 b</td>
<td>127.70 h</td>
</tr>
<tr>
<td></td>
<td>Maxima 14</td>
<td>6.27 a</td>
<td>1.83 de</td>
<td>17.37 cd</td>
<td>3.94 a</td>
<td>97.70 de</td>
</tr>
<tr>
<td></td>
<td>CAB 11E</td>
<td>6.42 a</td>
<td>1.76 de</td>
<td>15.24 b</td>
<td>4.12 def</td>
<td>97.433 de</td>
</tr>
<tr>
<td></td>
<td><em>Prunus avium</em></td>
<td>7.48 b</td>
<td>1.70 cd</td>
<td>17.73 d</td>
<td>3.93 a</td>
<td>112.067 g</td>
</tr>
</tbody>
</table>
night rehydration in all scion–rootstock combinations. Although the lowest %PFD, was recorded in trees grafted on invigorating Prunus avium (Table 4) as a result of the dense canopy, these plants had the highest %ΨMD. Trees on the most size-controlling rootstocks, Edabriz and Gisela 5, consistently had lower %ΨMD (Table 2) than trees on invigorating rootstocks, consistent with previous findings for cherry (Schmitt et al. 1989, Gonçalves et al. 2003), peach (Bongi et al. 1994, Basile et al. 2003) and apple (Giulivo and Bergamini 1982). This phenomenon is likely related to low water absorption capability of the root system of dwarfed trees compared with the transpiration demand of the canopy, or the high hydraulic resistance of the root system or graft union. Olien and Lakso (1986) favored the hydraulic limitation hypothesis (Ryan and Yoder 1997) to explain the lower %ΨMD of apple trees on dwarfing rootstocks compared with trees on invigorating rootstocks. In apple orchards, Cohen and Naor (2002) reported that differences in hydraulic conductivity resulted in differences in water use. Another explanation for the lower %ΨMD in cherry cultivars grafted on dwarfing rootstocks compared to the invigorating Prunus avium may be associated with differences in effective rooting depth among these rootstocks, and hence, water supply. This is consistent with the commonly held view that vegetatively propagated rootstocks establish a more spreading, shallower root system than seed propagated rootstocks (Shackel et al. 1997). Some recent studies have identified a partial xylem discontinuity in the scion–rootstock grafting point of dwarfed trees that could be responsible for a reduced water supply to plant organs (Sekse 1998).

At high %ΨMD, leaves of cherry trees grafted on Prunus avium, CAB 11E and Maxma 14 exhibited consistently higher values of A and g, than leaves of cherry trees grafted on dwarfing Edabriz or Gisela 5, but the cultivars on the dwarfing rootstocks had higher A/g, (Figure 1, Table 2), which is in accordance with previous reports for cherry (Shackel et al. 1997) and grapevine (Patakas et al. 2003). In our study, %ΨMD was positively correlated with A (r = 0.405, P < 0.01), g, (r = 0.473, P < 0.001) and C, (r = 0.504, P < 0.001) (Table 9) and negatively correlated with A/g, (r = −0.442, P < 0.001) (Table 9). Shackel et al. (1997) also showed a positive correlation between %ΨMD and A in cherry, and Naor (1998) and Naor et al. (1995) reported high correlations between %ΨMD, g, and productivity parameters in apple and other deciduous orchard species. As expected, A correlated positively with g, (r = 0.821, P < 0.001) (Table 9), and the data best fitted a hyperbolic function (r² = 0.62), indicating that the linear relationship between the parameters varied with size-controlling rootstock used (Figure 3). The slopes of the first-order linear regression between A and g, and the respective coefficients of determination increased from invigorating to dwarfing rootstocks, indicating that, for a given variation in g, the trees grafted on dwarfing Edabriz and Gisela 5 exhibited greater variation in %ΨMD than trees on invigorating Prunus avium, CAB 11E and Maxma 14. This relationship can be used to assess the effect of size-controlling rootstocks on gas exchange of sweet cherry trees under comparable environmental conditions.

Values of Ci, like %ΨMD, were lower in trees grafted on the dwarfing rootstocks than in trees grafted on invigorating rootstocks. Low Ci, in association with high A/g, values (Figure 1), indicates a greater effect of stomatal factors than non-sto-
maternal factors on photosynthetic capacity (Flexas and Medrano 2002). The high $A/g_s$ values in association with low $C_i$ and low $\Psi_{MD}$ in trees grafted on dwarfing rootstocks suggests the involvement of other mechanisms such as root–shoot hormonal signals, namely abscisic acid (ABA) synthesis, in the stomatal regulation mechanism in these trees. Although this finding is consistent with the well-documented phenomenon of non-hydraulic signalling (Zhang et al. 1997), it cannot be confirmed because we did not measure ABA concentration. Nevertheless, non-hydraulic signalling related to root-sourced ABA has been reported previously for Prunus (Fubeder et al. 1992, Correia et al. 1997).

The lower $A$ in cultivars on dwarfing rootstocks was associated with slight reductions in $F_v/F_m$, $F_o$, $F_m$ and $F_v$ (Figure 1, Table 3) compared with cultivars on invigorating rootstocks, indicating that down-regulation of PSII efficiency was associated with a protective increase in non-radiative dissipation of light energy (Oberhuber and Bauer 1991). Moreover, among the rootstocks, trees on dwarfing rootstocks had the highest concentrations of total carotenoids (Table 5), probably including xanthophyll cycle pigments, which have a photoprotective role in thermal energy dissipation (Demmig-Adams 1990, Ball et al. 1994).

Concentrations of total chlorophyll, Chl$\alpha$/Chl$\beta$, total carotenoids and total soluble sugars were highest in cherry trees grafted on dwarfing rootstocks, whereas starch and total phenolic concentrations were highest in trees on invigorating rootstocks (Tables 5 and 6). Despite having the highest concentrations of total chlorophyll, trees on dwarfing Edabriz and Gisela 5 presented the lowest $A$, which supports our assertion that stomatal control is the main cause of the variation in photosynthetic rates among the rootstocks.

**Effect of the physiology of the scion–rootstock interaction on fruit physicochemical characteristics**

The physicochemical characteristics measured in cherries from the three cultivars suggest that regulation of fruit quality is more dependent on the cultivar than on the rootstock (expressed as the percentage of total variation). However, the effect of the rootstock was statistically significant (Table 1). Several studies have shown that the rootstock affects fruit quality in other species. For example, in grapevine, the rootstock affected growth, yield and juice qualitative components (Paranychianakis et al. 2004). In sweet cherry trees, Moreno et al. (1996) reported that the invigorating rootstock Adara profoundly affected the fruiting response of ‘Van’ compared with the less invigorating rootstocks studied, SL 64 and Prunus mahaleb. In our study, ‘Summit,’ which had high values of $\Psi_{MD}$ and $A$, had the highest fruit mass, particularly when grafted on the invigorating rootstocks Maxma 14, CAB 11E and Prunus avium (Table 7). Furthermore, $\Psi_{MD}$ correlated

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**Table 9. Correlations (linear correlation coefficients) between physiological parameters and fruit quality characteristics of cherry cultivars ‘Burlat,’ ‘Summit’ and ‘Van,’ each grafted on rootstocks Edabriz, Gisela 5, Maxma 14, CAB 11E and Prunus avium.**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\Psi_{MD}$</th>
<th>$A$</th>
<th>$g_s$</th>
<th>$C_i$</th>
<th>$A/g_s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>0.405 **</td>
<td></td>
<td>0.473 ***</td>
<td>0.821 ***</td>
<td></td>
</tr>
<tr>
<td>$g_s$</td>
<td>0.504 ***</td>
<td>0.481 ***</td>
<td></td>
<td>0.692 ***</td>
<td></td>
</tr>
<tr>
<td>$C_i$</td>
<td>-0.442 ***</td>
<td>-0.777 ***</td>
<td></td>
<td></td>
<td>-0.851 ***</td>
</tr>
<tr>
<td>$A/g_s$</td>
<td>0.403 **</td>
<td>-0.152</td>
<td></td>
<td>-0.859 ***</td>
<td></td>
</tr>
<tr>
<td>$F$</td>
<td>-0.261 *</td>
<td>-0.296 *</td>
<td></td>
<td>0.184</td>
<td>0.202</td>
</tr>
<tr>
<td>$L^*$</td>
<td>0.008</td>
<td>-0.503 ***</td>
<td></td>
<td>-0.368 **</td>
<td>-0.213</td>
</tr>
<tr>
<td>$C^*$</td>
<td>0.019</td>
<td>-0.462 ***</td>
<td></td>
<td>-0.364 **</td>
<td>-0.206</td>
</tr>
<tr>
<td>SS</td>
<td>-0.026</td>
<td>0.087</td>
<td></td>
<td>0.073</td>
<td>0.011</td>
</tr>
<tr>
<td>TA</td>
<td>0.042</td>
<td>-0.003</td>
<td></td>
<td>0.053</td>
<td>0.047</td>
</tr>
</tbody>
</table>

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Figure 3. Relationship between photosynthesis ($A$) and stomatal conductance ($g_s$) in CAB 11E ($y = 9.933 + 0.006x$, $r^2 = 0.53$, $P < 0.001$), Edabriz ($y = 6.542 + 0.016x$, $r^2 = 0.71$, $P < 0.001$), Gisela 5 ($y = 4.527 + 0.020x$, $r^2 = 0.67$, $P < 0.001$), Maxma 14 ($y = 10.786 + 0.004x$, $r^2 = 0.40$, $P < 0.001$), Prunus avium ($y = 10.888 + 0.004x$, $r^2 = 0.35$, $P < 0.001$) and all data ($y = 6.213 + 0.017x - 6.37\times10^{-6}x^2$, $r^2 = 0.62$, $P < 0.001$). Measurements were taken throughout the diurnal period on July 9, 2003.
positively with fruit mass \((r = 0.403, P < 0.01)\), which means that heavier fruits were found in trees with better water status (Table 9). Stem water potential was also closely related to fruit growth in apple (Naor et al. 1995) and in pear (Shackel et al. 1997). In apple, in addition to fruit size, other important fruit quality factors were related to \(\Psi_{stems}\); for example, fruit soluble solids content and yellow color increased linearly with decreasing \(\Psi_{stems}\) (Shackel et al. 1997).

The effect of size-controlling rootstocks on fruit firmness and soluble sugar concentration did not follow a specific trend among the three cultivars (Table 7). We observed a distinct effect of dwarfing and invigorating rootstocks only in cherries from ‘Van’. ‘Van’ cherries had the highest firmness and soluble sugar concentrations when grafted on dwarfing rootstocks, which implies a high resistance to post-harvest damage and high consumer acceptability. As expected, soluble sugar concentration, titratable acidity and skin color were low in ‘Burlat’ (Tables 7 and 8), which is well known as an early-maturing cultivar with low sugar content and total acidity, and less red fruits. However, the quality of the fruits from ‘Burlat’ was enhanced when ‘Burlat’ was grafted on Maxma 14 or CAB 11E (Tables 7 and 8).

In our study, total soluble sugar concentration in leaves did not correlate with soluble sugar in fruits (data not shown). The earlyfruting habit in cherry suggests that a substantial portion of the carbohydrates necessary for early crop growth come from stored reserves in roots and stems; however, the importance of reserve carbohydrates could depend on the degree to which sweet cherry leaves have the capacity to photosynthesize under marginal environmental conditions during early spring (Roper and Kennedy 1986). Sweet cherry has a low light saturation point (Atkinson et al. 1997), which could be advantageous because CO\(_2\) assimilation could occur on cloudy days.

We found that \(A\) was negatively correlated with luminosity \((r = -0.503, P < 0.001)\) and chroma \((r = -0.462, P < 0.001)\) (Table 9). These findings indicate that the trees on invigorating Maxma 14, CAB 11E and Prunus avium that have the highest \(A\) also produced darker and redder fruits than trees on dwarfing Edabriz and Gisela 5.

We conclude that, when climatic transpirational demand was high, the low ability of the hydraulic system of the dwarfing rootstocks to supply water to the leaves led to a decrease in stem water potential and low \(g_s\). These responses control plant water deficits and maintain water potential in a range that does not endanger the hydraulic system (Tyree and Sperry 1989). The reduction in water potential reduced photosynthetic carbon uptake and growth potential, which may be the mechanism underlying dwarfing of cherry trees by rootstocks, as found for apple (Higgs and Jones 1990, Sperry 2000). Limited carbon uptake, however, does not necessarily reduce fruit yield, because we observed that reduced photosynthetic productivity on dwarfing rootstocks resulted in good yields and reduced vegetative growth (Cohen and Naor 2002).

Our results fit well with the two hypotheses presented in the Introduction. We conclude that physiological responses of sweet cherry trees are influenced by the rootstock, because trees on different size-controlling rootstocks had different water relations, gas exchange and vegetative growth. In addition, we observed that invigorating rootstocks led to improved water status and high photosynthetic capacity. However, the different physicochemical characteristics of cherries from the three cultivars suggest that regulation of fruit quality is more dependent on the cultivar, although the effects of rootstock genotype and cultivar \(\times\) rootstock interaction were also statistically significant. We conclude that the scion–rootstock combination is an important parameter to consider in orchard planting strategies.

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References


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